Hibernation and daily torpor in Australian mammals

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ABSTRACT

Torpor is the most effective means for energy conservation available to mammals and is characterized by substantial reductions in body temperature (T_b) and metabolic rate (MR). Most Australian terrestrial mammals are small with high mass-specific energy requirements and, although it is widely believed that torpor is not needed in a 'warm' country like Australia, a large number of species are heterothermic (i.e. capable of changing T_b, in contrast to homeothermic mammals with a constant high T_b). These heterothermic species (estimated >43% of terrestrial Australian native mammals) employ periods of daily torpor or prolonged multi-day torpor (hibernation) to conserve energy. Daily torpor is used by dasyurids (e.g. dunnarts, antechinus, quolls), myrmecobiids (numbat), tarsipedids (honey-possum), petaurid possums (e.g. sugar glider), rodents (but only known in the introduced house mouse), and small megabats (blossom-bats). During daily torpor, T_b is reduced from ~35°C during the active or normothermic phase to ~10-25°C during torpor, and the torpor MR (TMR) is ~30% of the basal metabolic rate (BMR). Daily torpor is often, but not exclusively, used during the rest phase and, between bouts of torpor, animals usually forage and feed. Recent evidence shows that free-ranging arid zone dasyurids may employ daily torpor on every day in winter and that torpor may last twice as long as in captivity (often up to around 20 hours), which will reduce energy expenditure and thereby food requirements by up to 80%. Hibernation or prolonged torpor has been observed in the Monotremes (echidna), marsupials (pygmy-possums and feathertail glider) and insectivorous bats (e.g. long-eared bats). During prolonged torpor, which often, but not exclusively, is expressed in winter, T_b is usually reduced to a minimum of ~0-10°C, and torpor bouts may last for several days or weeks, but in all species periodic arousals with brief normothermic periods (hours) between bouts of torpor have been observed. The TMR during hibernation is extremely low and can be as little as 1-5% of the BMR; daily energy expenditure can be reduced to only 3% of that in active individuals permitting survival on stored body fat for months without the need to feed. Daily and prolonged torpor in many Australian mammals appear to be opportunistic and not only important for survival of adverse seasonal conditions, but apparently also for dealing with unpredictable events such as droughts and perhaps fires and floods. As torpor substantially reduces energy requirements its use will in turn reduce the need for foraging and consequently exposure to predators. Predator avoidance by employing torpor and minimising foraging may be one of the reasons why none of the known heterothermic Australian species has gone extinct. In contrast many of the similar-sized perceived homeothermic species, such as rodents and bandicoots, have suffered high rates of extinction possibly because they must forage long and frequently to meet large energetic demands and thus are more vulnerable to predation by introduced foxes and cats.

Key words: body size, climate, conservation, energetics, thermal biology

Introduction

Australia is the continent with the taxonomically most diverse mammal fauna. The approximately 300 species of Australian terrestrial mammals belong to the three extant mammalian subclasses the Monotremata (Prototheria - egg-laying mammals, 2 species), Marsupialia (Metatheria - pouched mammals, ∼160 species), and Placentalia (Eutheria - placental mammals, bats ∼76 species, rodents ∼65 species) (Menkhorst and Knight 2001).

The majority (>94%) of native terrestrial Australian mammals are small (<10 kg) and consequently have a large relative surface area in comparison to the volume of their heat producing tissues. Because they are endothermic and regulate their body temperature (T_b) by producing metabolic heat internally to compensate for heat loss via their body surface, they must consume large amounts of food to fuel heat production while maintaining a high, constant T_b (Withers 1992; Bradshaw 2003). Therefore, in small mammals food requirements can easily exceed available resources (Hume 1999). These limitations are the main reason why not all endotherms are permanently homeothermic (permanent high and stable T_b of ∼32 to 38°C) and are capable of entering a state of torpor (Lyman et al. 1982; Wang 1989; Geiser and Ruf 1995; Lovegrove and McKechnie 2008).

Species capable of entering a state of torpor are often referred to as 'heterothermic endotherms'. When normothermic, heterotherms are able to maintain a high T_b via physiological thermoregulation, just like homeotherms. However, unlike homeotherms, they are also able to substantially reduce T_b, metabolic rate (MR) and water turnover by entering torpor usually during acute or potential energy or water limitations. Torpor

Theme edition of Australian Zoologist "*Ecology meets Physiology*", a Gordon Grigg festschrift, edited by Lyn Beard, Daniel Lunney, Hamish McCallum and Craig Franklin. Australian Zoologist Vol 35 (2) 2010.

saves energy because (i) thermoregulation at high T_b is abandoned and no energy is required for normothermic thermoregulation, (ii) because the T_b falls, temperature effects reduce the MR below the basal MR (BMR) and (iii) some species, especially those that are able to use prolonged multi-day torpor, can use metabolic inhibition in addition to temperature effects on MR to further minimise energy expenditure (Boyer and Barnes 1999; Guppy and Withers 1999; Geiser 2004). Consequently, MR can be reduced to a small fraction of BMR, which in normothermic individuals represents the minimum maintenance MR (Dawson and Hulbert 1970; Geiser and Ruf 1995), resulting in a substantial reduction in energy requirements. Although torpid individuals usually thermo-conform over a wide range of T_b, thermoregulation during torpor is not entirely abandoned. To prevent T_b falling to critical levels, the T_b during torpor is regulated at a species- or population-specific minimum T_b via a proportional increase of MR (Heller and Hammel 1972).

Two general patterns of torpor are widely recognised. The first of these, prolonged torpor or hibernation in the 'hibernators', occurs throughout the hibernation season usually lasting for about six months. Hibernation is characterised by a series of multi-day torpor bouts interrupted by periodic arousals followed by brief normothermic periods lasting for several hours (Wang 1989). However, at high T_a, hibernators may exhibit short bouts of torpor lasting for less than one day and may even forage between torpor bouts (Körtner and Geiser 2000a; Turbill and Geiser 2008). When exposed to low T_a, the T_b of torpid hibernators usually falls to values between 0 and 10°C, and the MR during torpor (TMR) is on average only 1 to 5% of the BMR. In hibernators extensive fattening or accumulation of food stores (the latter is not known to be used extensively in Australian mammals, but is common in e.g. sciurid rodents) generally precedes the torpor season, and many enter torpor only when they are fat. Daily torpor in the 'daily heterotherms' is the second common pattern. During daily torpor, which lasts for hours rather than days, T_b is usually maintained between 10 and 25°C and TMR is on average ~30% of BMR (Geiser and Ruf 1995). Daily heterotherms generally enter torpor when they are lean and often refuse to enter torpor when they are fat. 'Aestivation' is often used to describe daily or prolonged torpor at high T_a in summer, but since in mammals there is no evidence that it differs functionally from the other torpor patterns (Song et al. 1997; Geiser and Brigham 2000; Geiser 2009), aestivation is not specifically addressed in this article.

Traditionally, torpor in endotherms was seen predominantly as an adaptation of cold climate species and it is still widely believed that torpor and especially hibernation do not occur at all on the warm continent of Australia. However, it is now established that torpor is employed by many diverse terrestrial mammals from a wide range of habitats ranging from the arctic to the tropics including many Australian species (Barnes 1989; Geiser and Ruf 1995; Bartels et al. 1998; Lovegrove 2000; Fietz et al. 2003; Dausmann et al. 2005; Geiser 2003, 2006; Geiser and Körtner 2004; Stawski et al. 2008). The purpose of this review is to summarise what is known about torpor patterns in Australian mammals specifically, and how torpor use is likely to affect various aspects of their life including their conservation.

Monotremes

Torpor has been observed in the short-beaked echidna (*Tachyglossus aculeatus*, 2-7 kg), but not in the other Australian monotreme, the platypus (Grigg et al. 1992a,b, 2004; Grigg and Beard 2000; Nicol and Andersen 1996, 2000, 2007; Fig. 1). Echidnas are ubiquitous on the entire Australian continent and Tasmania. Echidnas have low T_b and MR even when active, and have been observed to enter prolonged torpor in many areas of Australia. Hibernation is most pronounced in the Australian Alps and Tasmania where the hibernation season may last for more than 6 months in the wild. In reproductive individuals hibernation is terminated in mid-winter when they mate, whereas non-reproductive individuals continue to hibernate until spring. During the hibernation season echidnas display prolonged torpor bouts with T_b <10°C lasting for about two weeks or more, and, as in other hibernators, these are interrupted by brief normothermic periods. Even in warm areas such as southwestern Queensland, echidnas remained torpid for up to 9 days during winter with T_b of ~14°C and occasionally for one day in summer (Brice et al. 2002). The TMR during torpor is extremely low and similar to that in other, including placental, hibernators, but because the BMR of echidnas is low the reduction of TMR in relation to BMR is smaller than in many other hibernators (Nicol et al. 1992) (Table 1). The low T_b and consequently MR during activity and the low TMR reduce both energy and water requirements and likely contribute to the continued success of the species in a large variety of habitats.

Marsupials

Torpor or heterothermy has been observed in three of the four orders of Australian marsupials, the Dasyuromorphia, the Notoryctemorphia, and the Diprotodontia. An estimated 43% of the Australian species are heterothermic (Fig. 1). Only the bandicoots (Peramelemorphia) are

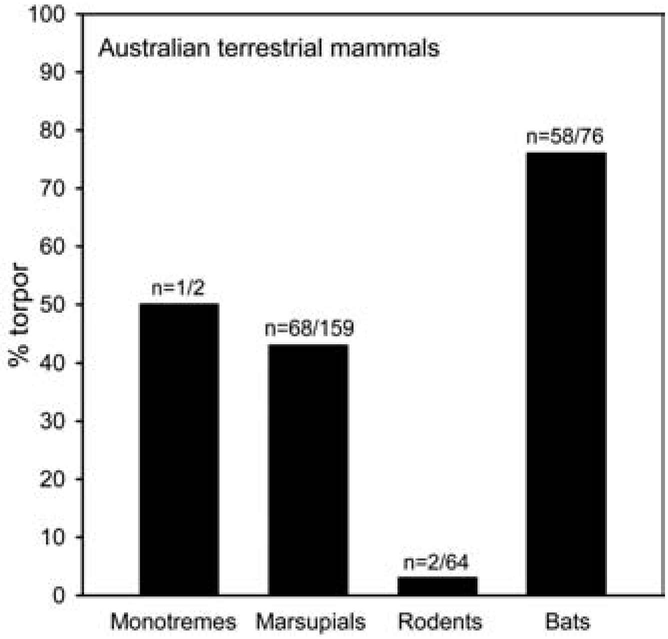

Figure 1. Known or estimated number of heterothermic species/all species of Australian terrestrial mammals. Numbers from Table 1.

Table 1. Summary of body mass and physiological variables in heterothermic Australian mammals

SUBCLASS **Order** **FAMILY, Genus species**	**Patterns of heterothermy**	**References** **(known or estimated number of heterothermic species/total species)**
MONOTREMATA (egg-laying mammals)		
TACHYGLOSSIDAE: *Tachyglossus aculeatus,* short-beaked echidna (2-7 kg)	Echidnas hibernate in many, including warm, areas of Australia, torpor bouts last for ~1-3 weeks, and short bouts of torpor may occur in summer. T_b falls to a minimum of ~4°C and TMR is ~10-20% of BMR. Hibernate up to 7 months, but may terminate hibernation in mid-winter for mating.	Martin 1902; Augee et al. 1970; Grigg et al. 1992a, 2004; Nicol & Anderson 1996, 2000, 2007; Grigg & Beard 2000; Falkenstein et al. 2001; Brice et al. 2002 (1/2)
MARSUPIALIA (pouched mammals)		
Dasyuromorphia (insectivorous/ carnivorous marsupials)		
DASYURIDAE: *Planigale* spp., planigales (5-15g); *Ningaui* spp., ningauis (9-12g); *Sminthopsis* spp., dunnarts (10-60g); *Antechinomys laniger*, kultarr (27g); *Pseudantechinus macdonnellensis*, fat-tailed antechinus (30g); *Antechinus* spp., antechinus (20-100g); *Dasycercus cristicauda*, mulgara (100g); *Dasyuroides byrnei*, kowari (120g); *Dasyurus* spp., quolls (1000g)	Dasyurids display daily torpor, with torpor bouts lasting ~2-20 h and T_b minima of ~11-25°C, with the lower T_b in the smaller species. TMR ~ 10-60% of BMR. Spontaneous torpor is common, but food restriction increases torpor use. Several species enter torpor throughout the year and some while pregnant/lactating or as juveniles. Arid zone dasyurids in the wild may enter torpor for up to 100% of days in winter and bask in sun during rewarming from torpor.	Godfrey 1968; Arnold 1976; Dawson & Wolfers 1978; Morton & Lee 1978; Wallis 1979; Geiser & Baudinette 1987, 1988; Geiser et al. 1986, 2002, 2006, 2008; Geiser 1988; 2003; Körtner et al. 2008; Warnecke et al. 2008 (53/55)
MYRMECOBIIDAE: *Myrmecobius faciatus*, numbat (500g)	Daily torpor in winter in the field and captivity with a minimum T_b to 19.1°C and torpor bouts lasting for up to 15 h.	Cooper & Withers 2004 (1/1)
Notoryctemorphia (marsupial moles)		
NOTORYCTIDAE: *Notoryctes caurinus,* marsupial mole (34g)	Captive individual heterothermic with unstable T_b ranging from 23 to 31°C.	Withers et al. 2000 (2/2)
Diprotodontia (possums and gliders)		
BURRAMYIDAE: *Cercartetus* spp. (10-35g), *Burramys parvus* (60g), pygmy-possums	All five species of pygmy-possums display torpor. Four species are known to hibernate with torpor bouts of ~1-4 weeks, T_b minima of ~1-6°C and TMR of ~3% of BMR. Prolonged torpor in *Cercartetus* is not strongly seasonal. *Burramys* hibernate for ~6 months under snow in the Australian Alps. *Cercartetus nanus* can hibernate for up to one year without access to food, the longest period known for any mammal.	Bartholomew & Hudson 1962; Geiser 1987, 1993, 2007; Geiser & Broome 1991; Song et al. 1997; Körtner & Geiser 1998; Geiser & Körtner 2004 (5/5)
ACROBATIDAE: *Acrobates pygmaeus*, feathertail glider (12g)	Can enter prolonged torpor for up to 1 week in captivity with a T_b minimum of ~2°C and TMR ~6% of BMR, but do not fatten in fall; appear to use both short or multi-day torpor bouts. Torpor physiology differs among individuals from different habitats.	Frey & Fleming 1984; Fleming 1985; Jones & Geiser 1992; Geiser & Ferguson 2002; Geiser & Körtner 2004 (1/1)

TARSIPEDIDAE: *Tarsipes rostratus*, honey possum (10g)	Displays short bouts of torpor in captivity of less than 1 day with a T_b minimum of 5°C and TMR ~ 5% of BMR. Torpor mainly occurs between March & September in animals captured in pitfall traps.	Collins et al. 1987; Withers et al. 1990 (1/1)
PETAURIDAE: *Petaurus breviceps*, sugar glider (130g); *P. australis*, yellow-bellied glider (600g); *Gymnobelideus leadbeateri*, Leadbeater's possum (120g)	*P. breviceps* display daily torpor in the wild with bouts of up to 23 h, a T_b minimum of 10.4°C and TMR ~10% of BMR. Sugar gliders are reluctant to enter torpor in captivity and torpor is much longer in wild than in captive individuals. Little is known about torpor in *G. leadbeateri* and *P. australis,* but anecdotal reports suggest they are heterothermic.	Fleming 1980; Smith 1980; Körtner & Geiser 2000; Geiser & Körtner 2004; Christian & Geiser 2007; Geiser et al. 2007 (5/6)
PLACENTALIA (placental mammals)		
Rodentia (rodents)		
MURIDAE: *Mus musculus*, house mouse (10-35g); *Pseudomys hermannsburgensis,* sandy mouse (11g)	Daily torpor occurs in feral mice in winter in the wild and in the laboratory with T_b minima of 18-22°C. Captive *Pseudomys* lower their T_b, in the cold, but this appears to be a hypothermic response rather than a controlled reduction of MR and T_b as during daily torpor.	Morton 1978; Predavec 1997; Tomlinson et al. 2007 (2/64)
Chiroptera (bats)		
PTEROPODIDAE: *Macroglossus minimus, Syconycteris australis*, blossom bats (16-18g); *Nyctimene robinsoni*, tube-nosed bat (~50g)	Blossom bats enter daily torpor in the light phase with T_b minima of 17-23°C. Torpor in captive *Syconycteris* is more pronounced in summer when nectar is less abundant than in winter. Tube nosed bats enter daily torpor.	Hall & Pettigrew 1995; Geiser et al. 1996; Bartels et al. 1998, Coburn & Geiser 1998; Geiser 2006 (4/12)
EMBALLONURIDAE: *Taphozous australis*, sheathtail bats (~25g)	*Taphozous* enter torpor in captivity with a minimum recoded T_b of ~16 °C.	Kulzer et al. 1970 (4/8)
RHINOLOPHIDAE: *Rhinolophus megaphyllus*, eastern horseshoe bat (8g)	Horseshoe bats enter torpor with a minimum recorded T_b of ~16°C.	Kulzer et al. 1970 (2/2)
HIPPOSIDERIDAE: *Rhinonicteris aurantius*, golden horseshoe bat (7g)	Captive *Rhinonicteris* enter torpor in the morning with a regulated T_b minimum of 23.6°C at T_a 17 °C. Exposure to T_a 10°C was lethal.	Kulzer et al. 1970 (6/6)
VESPERTILIONIDAE: *Myotis adversus* (8g); *Vepadelus* spp., forest bats (~5g); *Chalinolobus* spp., wattled bats (6-14g); *Scotorepens* spp. broad-nosed bats (7g); *Miniopterus schreibersii*, bent-wing bats (11g); *Nyctophilus* spp., long-eared bats (7-15g)	Hibernation is common in vespertilionids from southern Australia with T_b of ~1 to 15°C and TMR ~1-5% of BMR. Torpor bouts may last for more than 2 weeks and up to 5 days in subtropical areas, but some species forage during warm weather in winter. In summer, bats may remain torpid for several days during cool weather. Short bouts of torpor, often in the rest phase, are common in summer even in subtropical species.	Kulzer et al. 1970; Hosken and Withers 1997; Geiser & Brigham 2000; Turbill et al. 2003a,b; Willis et al. 2005; Turbill 2006; Geiser 2006; Turbill & Geiser 2005, 2008; Stawski et al. 2008 (36/36)
Molossidae: *Mormopterus loriae*, northern freetail bat (9g)	The northern freetail bat enters torpor with a minimum recorded T_b of 10°C.	Kulzer et al. 1970 (6/11)

T_b – body temperature; BMR – basal metabolic rate; TMR – torpor metabolic rate. Number of species from Menkhorst and Knight (2001).

currently considered to be homeothermic (Hulbert and Dawson 1974; Warnecke et al. 2007), perhaps because their omnivorous diet permits feeding throughout the year and most are substantially larger than the majority of Australian heterothermic mammals.

Dasyuromorphs

Insectivorous/carnivorous marsupials of the family Dasyuridae have been investigated in some detail with regard to torpor both in the laboratory and more recently in the field (Godfrey 1968; Wallis 1979; Dawson 1989; Dickman 1996; Geiser 2003; Körtner et al. 2008; Table 1). Known heterothermic dasyurids range in body mass from ~6 g in *Planigale* spp. to ~1,000 g in the western quoll, *Dasyurus geoffroii*. All heterothermic dasyurids that have been studied appear to employ daily torpor exclusively, with torpor bouts lasting for several hours from the late night or early morning to the following late morning or early afternoon. Moreover, dasyurids may enter two or more short torpor bouts per day occasionally. Some dasyurids employ torpor to reduce energy expenditure during reproduction when many other heterothermic mammals are strictly homeothermic, and some even employ torpor during development and growth suggesting that the use of torpor is of critical importance in this family (Geiser et al. 2008). Minimum T_b measured during torpor range from ~11 to 15°C in the small dasyurids (<100 g) and ~15 to 23°C in the larger species (>100 g). Minimum TMR range between 13 and 54% of BMR (Table 1), the reduction in daily energy expenditure by the use of torpor usually is in the range of 10 to 40% of individuals that remained normothermic at the same T_a, and water savings during torpor are also substantial (Frey 1991; Holloway and Geiser 1995; Song et al. 1995; Geiser and Drury 2003; Cooper et al. 2005). Daily torpor in captive dasyurids does not only occur at low T_a, but individuals may enter torpor at T_a between 25 and 30°C especially when food is withheld, although at high T_a torpor is shallow and brief (Song et al. 1995; Geiser 2003). Moreover, captive dasyurids, especially those from the arid zone, frequently enter spontaneous torpor (food available), which is likely to be an adaptation to the limited resource availability in their desert environment. Recent field data support this interpretation, with frequent (up to 100% of days in winter) and long torpor bouts, often about 20 hours/day, observed in free-ranging desert dasyurids (Geiser et al. 2002; Geiser and Pavey 2007; Körtner et al. 2008; Warnecke et al. 2008).

Dasyurids like other small daily heterotherms generally do not fatten substantially before the torpor season, and often lose mass before they will use torpor frequently (Morton 1978; Holloway and Geiser 1996). Dasyurids appear to rely on daily torpor predominantly to reduce foraging and food requirements (Geiser 2003), but small species cannot survive for prolonged periods without food (Kennedy and McFarlane 1971). This is clearly different from similar-sized small pygmy-possums, which can employ prolonged torpor and survive entirely on body fat stores and without food for months (Geiser 2007).

Whereas the MR during torpor is substantially reduced, endothermic rewarming from torpor at the end of a torpor bout is energetically expensive and, because in daily heterotherms occurs once or twice per day, reduces the savings accrued from daily torpor. In the field, desert dasyurids employ basking during rewarming from low torpor T_b in autumn and winter, apparently to reduce rewarming costs. Recent data on free-ranging arid zone dasyurids show that basking during rewarming from torpor occurs in at least four species (*Planigale gilesi* 8 g; *Sminthopsis crassicaudata* 10 g; *Sminthopsis macroura* 15 g and *Pseudantechinus macdonnellensis* 31 g). Basking commenced about 3 hours after sunrise when the T_b in individuals emerging from their burrows or resting sites to expose themselves to sunshine ranged from 13.8 to 19.3°C; these are the lowest T_b at which purposeful movement has been observed in any mammal (Geiser et al. 2002, 2008; Geiser and Pavey 2007; Warnecke et al. 2008). Apparently basking is used to minimize energy expenditure during arousal and to maximize energy savings gained from torpor (Geiser and Pavey 2007; Warnecke et al. 2008; Körtner et al. 2008). In the laboratory, basking during rewarming from torpor reduced rewarming costs by up to 85% (Geiser and Drury 2003; Warnecke and Geiser 2010), or, when exposed to a simulated natural morning increase of T_a, rewarming costs were reduced by about 65% (Lovegrove et al. 1999). A combination of the low TMR, access to solar energy during passive rewarming from daily torpor, and access to solar energy during the normothermic rest phase allows desert dasyurids to reduce daily energy expenditure by up to an estimated 80% (Warnecke et al. 2008). These savings are sufficient to limit foraging to a few hours after sunset and occasionally foraging can be omitted altogether (Körtner et al. 2008; Körtner and Geiser 2009). Thus, while the desert environment may be limiting with respect to food availability, the high T_a fluctuations and access to solar radiation provides small desert mammals with an alternative source of energy.

Daily torpor also occurs in numbats (*Myrmecobius fasciatus*, 500 g, Myrmecobiidae) both in captivity and in the field (Cooper and Withers 2004). Torpor usually commenced around or after midnight, torpor bouts lasted up to 15 hours and arousal occurred in the late morning. Generally the pattern of torpor and torpor depth exhibited by numbats appear similar to that in large dasyurids such as kowaris (Cooper and Withers 2004). However, basking during rewarming from torpor does not appear to be used by numbats (Cooper and Withers 2004). The species seems to use endogenous rewarming perhaps because radiant heat uptake is compromised by their size and risks from exposure to predators outweigh energy savings gained by basking.

Notoryctemorphs

Marsupial moles (*Notoryctes caurinus*, 34 g) are heterothermic (Withers et al. 2000). At T_a between 15 and 30°C, T_b of a captive individual was labile and the highest T_b measured was 30.8°C, well below that of other marsupials (Withers et al. 2000). Current data suggest that the marsupial mole like its ecological African equivalent, the golden mole (Fielden et al. 1990; Seymour et al. 1998), are thermal conformers with limited thermoregulatory capacity and may differ somewhat from the other heterothermic species described here.

Diprotodonts

Both prolonged torpor (hibernation) and daily torpor have been observed in the Diprotodontia. All pygmy-possums (small insectivorous/nectarivorous species of the family Burramyidae) that have been studied in some detail are capable of entering prolonged torpor. At low T_a, torpid pygmy-possums lower T_b to a minimum of ~2-6°C, their minimum TMR is only ~2-4% of BMR (Table 1), and they can remain torpid for up to 4 weeks at a time. The eastern pygmy-possum, *Cercartetus nanus* is capable of enormous fattening and, when maintained at T_a 7ºC, can hibernate for up to an entire year without access to food (Geiser 2007). It appears that torpor in pygmy-possums of the genus *Cercartetus* is not strongly seasonal. Prolonged torpor can be induced at any or most times of the year by exposing individuals to low T_a and in the wild short bouts of torpor have been observed in autumn when conditions were mild (Geiser and Körtner 2004). Even at the relatively high T_a of 19°C, torpor bouts lasting for two days were observed in captive *Cercartetus lepidus*. At even higher T_a of 26 to 30ºC, *Cercartetus nanus, C. concinnus* and *C. lepidus* still enter torpor, although at these T_a torpor lasted only for part of the day and TMR was ~50% of BMR (Geiser 1987; Song et al. 1997). It therefore appears that in *Cercartetus* spp. torpor use is an adaptation to unpredictable adverse changes in weather and food availability at any time of the year rather than or in addition to a predictable winter.

The mountain pygmy-possum, *Burramys parvus*, the largest species of the family, is restricted to high altitudes in the Australian Alps where it lives in deep boulder fields and feeds predominantly on Bogong moths in summer and on little or nothing in winter (Broome 2001). Hibernation in the species is more seasonal than in the other species (Geiser and Broome 1991,1993; Körtner and Geiser 1998; Geiser and Körtner 2004). The hibernation season begins in late autumn (April/May) with the departure of Bogong moths from the Australian Alps and lasts until the snow melts in spring September/October (Körtner and Geiser 1998). As in other hibernators (including the short-beaked echidna), reproduction commences immediately after the hibernation season (Lyman et al. 1982), and in order to increase mating success, males, which often hibernate on north-facing sun-exposed slopes, emerge from hibernation before females (Körtner and Geiser 1998). In captivity, juveniles begin to hibernate later than adults and, both in captivity and in the field, torpor bouts in females tend to be deeper and longer than in males (Geiser and Broome 1991; Körtner and Geiser 1998) possibly also a result of the spatial segregation of the sexes and exposure to different microclimates in the wild.

The pattern of hibernation and energy expenditure in *B. parvus* is strongly temperature-dependent as in other hibernators (Geiser and Kenagy 1988). Above T_a 2°C, torpor bout duration, T_b and MR and therefore energy expenditure fall with T_a. In contrast, a slight further reduction of T_a to 0°C, results in a substantial increase of MR of torpid individuals to stabilise T_b at about 2ºC, and bouts of torpor are reduced to about half, which requires frequent and costly rewarming (Geiser and Broome 1993). Thus, energy expenditure and use of stored fat is lowest at a T_a of about 2°C, as experienced by *B. parvus* in their snow-covered boulder field in winter (Körtner and Geiser 1998), and, at that T_a, animals are most likely to survive on their limited amount of stored fat (Geiser and Broome 1993). Higher and especially slightly lower T_a, which could be caused by lack of snow cover, increase arousal frequency and associated energy costs and also raise MR for thermoregulation during torpor. The result is a likely depletion of body fat stores well before spring (Geiser and Broome 1993). As winter mortality in the species is already high and the species is endangered (Mansergh and Broome 1994; Broome 2001), a change in climate is likely to have a detrimental impact on their hibernation pattern and thus winter survival, and possibly drive the species to extinction.

Torpor in the feathertail glider (*Acrobates pygmaeus*, Acrobatidae) has been studied in the wild and in captivity (Frey and Fleming 1984; Fleming 1985; Jones and Geiser 1992; Geiser and Ferguson 2001). In captivity, torpor in *A. pygmaeus* lasted for a maximum of 8 days, the minimum T_b was 2°C, and the TMR was only about 1% of that in normothermic animals at T_a 5°C and 6% of the BMR (Geiser et al. 1992; Jones and Geiser 1992; Geiser and Ferguson 2001). Thus, there are some similarities between the pattern of torpor in the feathertail glider to those of the burramyids. Nevertheless, it appears that *A. pygmaeus* does not have a prolonged hibernation season. Free-ranging feathertail gliders inhabiting cable junction boxes near Melbourne, Victoria entered torpor between March and November, but aroused daily (autumn to spring; Frey and Fleming 1984). Although prolonged torpor was not observed in the wild (Frey and Fleming 1984) it is likely that it is used during cold-spells or at high altitude, although a prolonged hibernation season seems unlikely. *Acrobates pygmaeus* also does not show extensive fattening, which contrasts to several of the burramyids and many other hibernating mammals. Perhaps the agility required for this diminutive gliding animal precludes the accumulation of large body fat stores similar to bats.

The honey-possum *Tarsipes rostratus*, the single species of the family Tarsipedidae, has been observed to use torpor in the wild. Torpor in individuals caught in pitfall traps occurred mainly during the cold season between March and September, but a few individuals were torpid even in summer between December and February (Collins et al. 1987; Withers et al. 1990; Bradshaw et al. 2007). In captivity, the species exhibited very low T_b of about 5°C, similar to that of hibernators, but torpor bouts did not exceed 10 hours (Withers et al. 1990). The TMR was about 5 times that in pygmy-possums and twice that in feathertail gliders, suggesting functional differences among these families.

In the sugar glider, *Petaurus breviceps* (Petauridae), spontaneous torpor (food *ad libitum*) was rarely observed in the laboratory and, even when food was withheld, individuals were reluctant to enter torpor (Fleming 1980; Dawson and May 1984; Geiser et al. 2007). Minimum TMR of sugar gliders measured in captivity were about 10% of those in normothermic, resting individuals and about twice those of pygmy-possums (Fleming 1980).

In contrast, free-ranging sugar gliders from a cool-temperate area displayed much more frequent and deeper torpor than individuals in captivity. Daily torpor, interrupted by arousal around dusk, often was observed over a sequence of several days, torpor bouts lasted for up to 23 hours (average 13 hours), and T_b fell as low as 10.4°C (Körtner and Geiser 2000b; Christian and Geiser 2007; Geiser et al. 2007). In winter (May to October), free-ranging sugar gliders entered torpor on about 17% of observation days in a wet year and torpor was common during cool, wet nights (Körtner and Geiser 2000b). However, in dry years in the same area, torpor frequency can be considerably lower (Christian and Geiser 2007). In comparison to free-ranging gliders, captive individuals kept outdoors under similar thermal conditions entered torpor only occasionally, and torpor was shorter (about 7 hours) and shallower (minimum T_b 18.5°C) than in the field (Geiser et al. 2007).

Torpor has also been observed in the Leadbeater's possum, *Gymnobelideus leadbeateri* (Smith 1980) and the rather large yellow-bellied glider, *Petaurus australis* (Table 2), but little is known about the patterns of torpor in these species.

To our knowledge, torpor has not been observed in the relatively large diprotodontids such as wombats (Vombatidae), koalas (Phascolarctidae), large possums (Phalangeridae), ringtail possums (Pseudocheiridae), rat kangaroos (Potoroidae and Hypsiprymnodontidae), and kangaroos (Macropodidae). Nevertheless, a low resting T_b of about 31°C has been observed in hairy-nosed wombats (Wells 1978).

Placental mammals

Rodents

In contrast to small marsupials, little is known about torpor in Australian rodents (Fig. 1). Unequivocal observations on daily torpor are only available for introduced house mice, *Mus musculus*, in winter (Table 1), which were found sharing nests with *Sminthopsis crassicaudata* in the wild (Morton 1978). Daily torpor in the species also has been observed in the laboratory in wild-caught and laboratory-bred *Mus*, which reduced T_b during torpor to about 20ºC, but also often became hypothermic (Tomlinson et al. 2007). The claim that sandy inland mice, *Pseudomys hermannsburgensis* enter torpor in the laboratory (Predavec 1997) has been questioned (Tomlinson et al. 2007), because they were unable to rewarm from low T_b. It appears that *Pseudomys* become hypothermic (failure in thermoregulation) rather than torpid (controlled reduction of T_b and MR) when exposed to cold (Tomlinson et al. 2007), which supports our observations (Drury, Seckerdiek, McAllan, Geiser unpublished; however, the unusual tolerance of hypothermia in this species surviving two days of hypothermia is intriguing and warrants further investigation). Nevertheless, as Australian rodents are diverse, and many rodents on other continents use torpor extensively (Lyman et al. 1982) it is possible that some Australian species, perhaps those feeding on unreliable food sources, do employ torpor for energy conservation.

Bats

Flying is energetically demanding, adding to the already high thermoregulatory and maintenance energy expenditure of a small mammal. It is therefore not surprising that torpor occurs in both mega- and microchiropterans in six of the seven Australian families and we estimate torpor is used by at least 76% of all Australian bat species (Fig. 1).

Megachiropterans (Megabats)

Contrary to the widely held view in the past that megabats are strictly homeothermic, recent work shows that three small Australian pteropodids, with a body mass of up to about 50 g, are capable of displaying daily torpor. These species (blossom-bats *Syconycteris australis*, *Macroglossus minimus* and the tube-nosed bat *Nyctimene robinsoni*), measured in captivity, all originated from tropical and subtropical regions. However, available data suggest that captive large megabats are homeothermic (Morrison 1959; Kulzer et al. 1970).

The largely nectarivorous Australian blossom-bats (Law 1994) appear to use daily torpor. In the laboratory, torpor usually commenced in the morning soon after lights on and lasted for several hours. Both *Syconycteris australis* and *Macroglossus minimus* entered induced torpor when food was withheld even at T_a as high as 25°C, and spontaneous torpor (food *ad libitum*) was observed at T_a 20°C. Arousal from torpor in undisturbed bats usually occurred between midday and the afternoon (Geiser et al. 1996; Bartels et al. 1998). Torpor in *S. australis* (18 g) from a subtropical region was deeper than in *M. minimus* (16 g) from a tropical region. The T_b of torpid *S. australis* was regulated at a minimum of about 18°C, whereas in *M. minimus* the minimum T_b was about 23°C (Geiser et al. 1996; Bartels et al. 1998). This suggests that the depth of torpor, and specifically the minimum T_b, is affected by the minimum T_a that a species or population normally encounters through its range, as has been suggested for birds (Wolf and Hainsworth 1972).

Mammals from cool northern climates generally show deeper and more frequent torpor in winter than in summer (Wang 1989; Carey et al. 2003). Seasonal changes in the use of torpor by *Syconycteris australis* from the subtropical east coast of New South Wales were the opposite. In winter, *S. australis* exhibit short torpor bouts (average 5.5 hours) and high minimum TMR (about 55% of BMR), whereas in summer, torpor bouts were long (average 7.3 hours) and the minimum was TMR low (about 35% of the BMR; Coburn and Geiser 1998). This unexpected pattern appears to be explained by day length and food availability. In the mild subtropical winter, bats can forage for prolonged periods during long nights and have access to an abundance of flowering plants (banksias in the costal heath flower mainly in winter). In summer, nights and thus foraging times are brief and the availability of nectar is substantially reduced (Coburn and Geiser 1998). Thus, the unusual seasonal pattern of torpor use in *S. australis* appears to be an appropriate physiological adaptation to ecological constraints of their subtropical habitat.

Microchiropterans (Microbats)

As the name suggests, microbats are on average smaller than megabats and contain some of the smallest mammal species. Of six families of Australian microbats only the family that contains the largest species, the ghost bat, *Macroderma gigas* (Megadermatidae), appears to be homeothermic (Leitner and Nelson 1967). The five remaining families (largely insectivorous Microchiroptera; Menkhorst and Knight 2001) all contain known heterothermic species, but most of the data are available on the family Vespertilionidae (Kulzer et al. 1970; Hall 1982; Geiser 2006; Table 1). Long-eared bats (*Nyctophilus geoffroyi* and *N. gouldi*), wattled bats (*Chalinolobus gouldii*), broad-nosed bats (*Scotorepens balstoni*) and forest bats (*Vespadelus vulturnus*) show low minimum T_b of ~1 to 6°C and TMR (~1-4% of BMR) that are similar to those of hibernating bats elsewhere as well as echidnas and pygmy-possums (Hock 1951; Geiser 2004).

In winter, free-ranging *N. geoffroyi* and *N. gouldi* can remain torpid for up to two weeks in the cool-temperate New-England region of NSW. However, night-time foraging does occur between torpor bouts during warm weather in winter (Turbill and Geiser 2008). Moreover, as these species roost in tree hollows or behind bark and are exposed to prevailing fluctuating T_as, partial or full passive rewarming is common around midday (Turbill and Geiser 2008). Observations of reduced trap success of bats in general (Lumsden and Bennett 1995; Brigham and Geiser 1998), and reduced activity in winter (Ellis et al. 1991), suggest that prolonged torpor is common in bats living in southern Australia. Even the subtropical *N. bifax* remained torpid for up to 5 days on the NSW north coast in winter (Stawski et al. 2008).

Torpor in microbats is not restricted to the cold season or cool weather although during summer bats are usually active for most of the night. For example, during summer on the New England Tablelands, even when daily maximum T_a approached 30°C, torpor during the morning was observed on 100% of roost days in *Nyctophilus* and a second bout of torpor in the afternoon was common (Turbill et al. 2003a,b). Furthermore, prolonged bouts of torpor (2 days) were observed during cool weather in summer (Turbill et al. 2003a,b). In captivity, torpor in tree-roosting *N. geoffroyi* may occur at T_a as high as 27°C, well above the hibernaculum T_a of many bats (Webb et al. 1996) with a substantial drop of TMR to 25% of BMR (Geiser and Brigham 2000). The occurrence of summer torpor may seem especially surprising for free-ranging subtropical *Vespadelus pumilus*, because food appeared to be abundant and T_a was mild (Turbill et al. 2003b). In subtropical *Nyctophilus bifax*, summer torpor was most frequent and pronounced in individuals in good body condition, suggesting that these bats use torpor for predator avoidance when they do not need to feed (Stawski and Geiser 2010). Thus even in the subtropics in summer torpor appears to be a normal part of these bats' daily routine, despite an apparent lack of thermal or nutritional stress, suggesting that torpor is part of everyday energy budgeting rather than an emergency measure. Considering the high MR during activity in comparison to the low TMR of microbats, especially prolonged torpor will result in enormous reduction in energy requirements.

Torpor use and the conservation of mammals

As we have seen in this article, torpor use plays an important role in the life of many small Australian mammals. The reduction of energy requirements afforded by torpor directly affects food and water requirements and thus survival of adverse conditions, but also can minimise foraging activities and consequently exposure to predators. Therefore, torpor use can contribute to an optimised foraging strategy in a way that is likely to have positive impacts on the ecological success of a species (Pavey and Geiser 2008). The apparent inability to use torpor seems to have detrimental effects on the long-term persistence of small homeothermic species, such as rodents, bandicoots and small macropods in the face of predation by introduced carnivores (Johnson 2006; Pavey et al. 2008). These groups, which do not possess substantial energy-conserving mechanisms, must forage under all conditions and therefore are exposed to predation for longer periods of time. These homeothermic small mammals are the worst affected Australian mammalian taxa with regard to extinction (Johnson 2006), whereas not a single known Australian heterothermic species, although some have suffered range reductions, has gone extinct (Geiser and Turbill 2009). Overall, homeothermic mammals in Australia (n=18, Johnson 2006) suffered a significantly higher rate of extinction (Chi-Square test; $p<0.0001$) than known heterothermic mammals (n=0). On the other hand, although torpor will help small mammals to overcome adverse conditions, use of torpor make these heterothermic species potentially susceptible to a number of human activities. For example, tree felling in winter likely will have a more negative effect on torpid rather than active possums or bats, because the former will be slow to respond to disturbances and perhaps unable to flee. Controlled burns in winter may have similar negative influences on many heterothermic species that may not act fast enough when they are in torpor. For the rare mountain pygmy-possum, which persists at high altitudes primarily because of its ability to hibernate, human activities may have complex impacts. For example, compacting of snow by grooming machines or production of artificial snow could delay snowmelt and prolong snow cover and thus winter. While the former example is likely to be localised, climate change, which is likely to reduce snowfall in the Australian Alps, may expose possums to large temperature fluctuations. These in turn are likely to interfere with normal hibernation of mountain pygmy-possums and may increase winter mortality. Thus, although torpor is a physiological adaptation that primarily results in a substantial reduction in food and water requirements, its use affects the behaviour and ecology of mammals and clearly has implications for their conservation.

Acknowledgements

We would like to thank Bronwyn McAllan and Chris Pavey for constructive comments on the manuscript and the Australian Research Council for supporting our work.

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